

Response diversity of wild bees to overwintering temperatures

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Abstract Biodiversity can provide insurance against environmental change, but only if species differ in their response to environmental conditions (response diversity). Wild bees provide pollination services to wild and crop plants, and response diversity might insure this function against changing climate. To experimentally test the hypothesis that bee species differ in their response to increasing winter temperature, we stored cocoons of nine bee species at different temperatures during the winter (1.5–9.5 °C). Bee species differed significantly in their responses (weight loss, weight at emergence and emergence date). The developmental stage during the winter explained some of these differences. Bee species overwintering as adults generally showed decreased weight and earlier emergence with increasing temperature, whereas bee species overwintering in pre-imaginal stages showed weaker or even opposite responses. This means that winter

warming will likely affect some bee species negatively by increasing energy expenditure, while others are less sensitive presumably due to different physiology. Likewise, species phenologies will respond differently to winter warming, potentially affecting plant–pollinator interactions. Responses are not independent of current flight periods: bees active in spring will likely show the strongest phenological advances. Taken together, wild bee diversity provides response diversity to climate change, which may be the basis for an insurance effect.

Keywords Insurance hypothesis · Climate change · Global warming · Hibernation · Phenology

Introduction

The consequences of global climate change for natural ecosystems can be severe (Sala et al. 2000; Parmesan 2006) and may affect their functioning and services (Geyer et al. 2011). Biodiversity is threatened by climate change (Thomas et al. 2004), but it may also provide an insurance against environmental variation (Naeem and Li 1997; Yachi and Loreau 1999) including climate change. If species respond differently to climate, the function performed by diverse communities should be more persistent across different climatic conditions than the function performed by species-poor communities. This property is generally called ‘response diversity’ (Elmqvist et al. 2003; Hooper et al. 2005; Laliberte et al. 2010), but it has been rarely tested whether species within functional groups really differ in their response to environmental change. In contrast, many studies on insect physiology rely on single model species (but see Addo-Bediako et al. 2002; Janion et al. 2009; Diamond et al. 2012). Pollination is an essential component

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of both ecosystem functioning and services (Kearns et al. 1998; Klein et al. 2007), and bees are the most important taxon contributing to this process (Kearns et al. 1998).

The phenology of many organisms is influenced by temperature. Increased temperature advances several phenological events (Fitter and Fitter 2002; Visser and Both 2005; Parmesan 2006), but the extent and direction of phenological shifts may vary between species (Fitter and Fitter 2002), potentially disrupting species interactions by phenological mismatch. While there are concerns about the integrity of plant–pollinator interactions (Memmott et al. 2007), field experiments show limited effects of phenological shifts on flower visitation (Parsche et al. 2011; Rafferty and Ives 2011).

Temperatures are predicted to increase disproportionately during the winter at least in Europe (Christensen et al. 2007). Effects of temperature during wintering are less studied than effects of temperature during periods of activity. Generally, metabolic rate increases with temperature (Brown et al. 2004), which might lead to increased loss of stored energy in overwintering animals. Negative effects of increasing winter temperature have been shown for a few insect groups (e.g. flies: Irwin and Lee 2003; butterflies: Fartmann and Hermann 2006). While dependence of bee activity on temperature during the activity period is well known (Corbet et al. 1993; Stone 1994; Vicens and Bosch 2000), responses to winter temperature have only been studied in a few bee species with a focus on improving commercial management (Krunic and Hinks 1972; Richards et al. 1987; Bosch et al. 2000; Bosch and Kemp 2003, 2004; Sgolastra et al. 2010; Pitts-Singer and Cane 2011). These studies have shown that overwintering temperature influences the time of adult emergence and possibly survival and weight loss. In the studied species, higher temperatures tended to advance emergence and increase mortality and weight loss. Bee emergence time is also influenced by temperature during spring (Kemp and Bosch 2000; White et al. 2009; Forrest and Thomson 2011; Bartomeus et al. 2011). However, previous studies tested only a few contrasts of overwintering temperature, mostly outside the range of likely environmental change or natural interannual variation, and none of them tested multiple species within a single study.

In this study, we experimentally investigated the effect of overwintering temperatures on different wild bee species, focusing on the potential effects on weight loss and changes in phenology (date of emergence). Using a finely resolved temperature gradient, we tested the hypothesis that there is response diversity in the reaction to temperature among bee species (as one of two conditions required for an insurance effect of bee diversity; the other condition, functional redundancy, was not explicitly tested here).

Materials and methods

Experiment

We performed an experiment with overwintering cocoons or brood cells of nine species of solitary wild bees (Hymenoptera: Apiformes: Megachilidae and Colletidae; Table 1) in climate chambers with a temperature gradient from 1.5 to 9.5 °C (at approximately 1 °C intervals). This gradient spans the whole range of temperature increases predicted by the IPCC (model projections for winter temperature increases in Northern Europe range between 2.6 and 8.2 °C under the A1B scenario; Christensen et al. 2007). Given that the recent average temperature in Göttingen for November to February is 2.5 °C, our experimental gradient mainly simulated different degrees of warming and only limited cooling.

We used 17 climate chambers situated in different departments of the University of Göttingen. Climate chambers included true climatic chambers (or cabinets) of different types (12), but also cold storage rooms (2) and refrigerators (3); all cooling devices are considered as ‘climate chambers’ in this paper. All were set to a constant mean temperature between 1.5 and 9.5 °C. To avoid bias by the different types of climate chambers, we also chose temperature settings to create a temperature gradient within each type and location of climate chamber. Apart from this constraint, temperatures were randomly assigned to climate chambers. One control set of bees was kept under outside conditions in Göttingen, Germany. Temperatures in each climate chamber were measured with iButton® data loggers every 90 min throughout the overwintering period. Mean temperatures across all measurements were used as explanatory variable in all analyses (=‘overwintering temperature’). The range of realized temperatures within a climate chamber was generally low (standard deviation of 90-min interval measurements: 0.04–2.04 °C), with slightly higher within-day fluctuations in refrigerators than in other devices.

Bee nests were acquired from trap nests placed in 2009 in the field, mostly at the experimental field of the Agroecology group in Göttingen, Germany, and at an apple orchard close to Leipzig, Germany (see Gruber et al. 2011 for details of the study site). Before the start of overwintering treatments, nests were stored in an unheated shed. Bee brood cells were isolated from the reed or bamboo internodes of the trap nests. Apparently intact brood cells were distributed in equal proportions to the different climate chambers. The same number of individuals and species proportion was used for all climate chambers (as far as possible). Individuals from the same nest were assigned to different climate chambers. Additionally, cocoons of two species (*Osmia bicornis* and *Osmia cornuta*) were purchased from the open rearing

Table 1 ANOVA tables of the linear mixed effects models of overwintering treatment effects on different bee species

	Num. <i>df</i>	Den. <i>df</i>	<i>F</i> value	<i>p</i> value
(a) Response variable: bee weight loss. i.e. log(fresh weight change pre- to post-winter in %); data were only available for <i>Osmia bicornis</i> and <i>Osmia cornuta</i>				
Species	1	550	12.3	<0.001
Temperature	1	14	51.9	<0.001
Relative humidity	1	14	14.4	0.002
Incubation days ^a	1	550	49.5	<0.001
Interactions				
Species × temperature	1	550	4.9	0.027
(b) Response variable: bee dry-weight after winter. i.e. log(weight in mg); includes nine bee species				
Species	8	775	4,775.8	<0.001
log(head width)	1	775	12,203.2	<0.001
Sex	1	775	82.8	<0.001
Meconium ^a	1	775	192.0	<0.001
Temperature	1	15	5.8	0.030
Interactions				
Species × log(head width)	8	775	4.6	<0.001
Species × sex	8	775	6.4	<0.001
Species × temperature	8	775	5.2	<0.001
(c) Response variable: bee phenology. i.e. days to adult emergence after winter; includes nine bee species				
Species	8	1,050	15,788.7	<0.001
Sex	1	1,050	1,429.8	<0.001
Temperature	1	15	163.1	<0.001
Interactions				
Species × sex	8	1,050	81.1	<0.001
Species × temperature	8	1,050	50.2	<0.001
Sex × temperature	1	1,050	27.9	<0.001
Species × sex × temperature	8	1,050	5.9	<0.001

^a *Incubation days* is the number of days from when the incubation of all bees was started to the time the bee was weighed after winter

^b *Meconium* refers to whether or not the bee had deposited meconium (a faeces-like residue) after emergence

facilities of WAB Mauerbienenzucht in Konstanz, Germany. These cocoons were treated identically to the brood cells isolated from trap nests. Brood cells were individually placed in ID-labelled glass test tubes and sealed with cotton wool. Cocoons of *Osmia* were weighed before overwintering. Pre-winter weight could not be reliably measured for the other species, in which cocoons were not present or could not be feasibly separated from other nesting material.

Overwintering was started on 5 November 2009, locating trays with bee test tubes in the climate chambers, and lasted until 1 March 2010, when all trays were brought to an incubation room with a temperature of 12–17 °C (partly following variation in outside temperature) and 42 % relative humidity. Test tubes were checked at least daily for emerged bees. During the first 5 days from the start of incubation, cocoons of *Osmia* were weighed again on the same scales, successively taking sets of bees from all climate chambers to avoid imbalance or bias. Emerged bees were killed with ethyl acetate and stored at –18 °C. On 20 April 2010, remaining bees were moved to a different incubation room with a temperature of 17–23 °C until all bees had emerged (22 June 2010).

In total, nine bee species were represented by at least ten emerged individuals and considered in the analyses. They can be broadly separated in two groups according to the developmental stage during the winter: *Osmia bicornis* (Linnaeus 1758), *Osmia cornuta* (Latreille 1805) and *Chelostoma florissomme* (Linnaeus 1758) enter diapause after initiating metamorphosis (overwintering as adult or late pupal stage, adult hereafter) and emerged earlier than 50 days after termination of wintering treatments, whereas *Heriades truncorum* (Linnaeus 1758), *Megachile ligniseca* (Kirby 1802), *Megachile centuncularis* (Linnaeus 1758), *Megachile versicolor* Smith 1844, *Hylaeus communis* Nylander 1852 and *Coelioxys mandibularis* Nylander 1848 overwinter as larva (prepupa) and emerged later than 50 days after end of wintering. The adult-overwintering species are naturally active in spring ('spring bees'), while the species that finish metamorphosis after winter are naturally active later in the year (late spring or summer; 'summer bees').

Dry weight was determined by drying specimens for 48 h (60 °C) and immediately weighing dried specimens (within 20 min after taking them from the drying oven, avoiding water absorption). Body size was measured for all

specimens as maximum head width in mm, as this measure has been previously shown to be the best correlate of body mass among a number of morphometric variables (Bosch and Vicens 2002).

Mortality during the winter was generally very low (less than 5 % in *Osmia bicornis* and *Osmia cornuta*; see Electronic Supplement), or it was difficult to separate from pre-winter mortality (including damage caused by handling). This applied especially to species overwintering in pre-imaginal stages, which had the additional problem that only developed specimens (i.e. survivors) could be assigned unequivocally to a species in most cases. Therefore, we consider only surviving individuals in all analyses.

Analyses

Statistical analyses were performed using the statistical software R v.2.11.1 (R Development Core Team 2010) and the ‘nlme’ package (Pinheiro et al. 2011). We used linear mixed effects models including a random effect of ‘chamber ID’ to be able to test for the interaction between species and temperature without pseudoreplication for the temperature treatment. This approach is similar to the test for response diversity used in Winfree and Kremen (2009). A variance function (different standard deviation per species) was used to assure homogeneity of variances (Pinheiro et al. 2011).

We used mean temperature as explanatory variable in all linear models. For more accurately predicting the metabolic effects of temperature, it might be argued that the non-linear relationship between temperature and metabolism should be considered. To explore whether this non-linearity might influence our results, we calculated the sum of estimated metabolic rate for each measured temperature (based on exponents given in Brown et al. 2004). This measure was highly correlated to mean temperature ($r = 0.995$) showing that the temperature–metabolism relationship is approximately linear for the range of temperatures explored here, so we stick to mean temperature in the rest of the paper.

All explanatory variables of the respective models (one for each response variable, i.e. weight loss, weight at emergence and time to emergence) are presented in Table 1. To control for effects of body size on body weight, we used head width as a covariable in the models explaining dry weight. Body size might still change in bee species that have not completed metamorphosis before the winter. However, head width was not affected by temperature in our experiment ($p > 0.5$ for both the main effect of temperature and for the temperature by species interaction; mixed effects model with head width as response variable, including only bees overwintering in pre-imaginal stages). In the dry weight model, we also included the

factor ‘meconium’, indicating whether a bee had defecated (i.e., deposited meconium) after hatching and thereby lost some weight.

In weight loss models (fresh weight) for *Osmia* species, relative humidity (not significantly correlated with temperature across climate chambers, $r = -0.26$, $p = 0.31$, $n = 17$) and the number of days from beginning of incubation to weighing of cocoons were used as covariables. The response variable was the logarithm of weight loss during winter as percent of pre-winter weight. No variance function was used in this model.

Results

Overwintering temperature did not influence mortality during winter, which was generally low (Online Resource, Table S1). However, overwintering temperatures affected both the weight after winter and the date of emergence. Differences among bee species were found for both responses, indicated by the significant interactions between temperature and species (Table 1).

The two species in which weight loss over the winter could be directly measured lost significantly more weight at higher overwintering temperatures (Fig. 1; Table 1). This effect was significantly stronger in *Osmia cornuta* (significant species \times temperature interaction), in which weight loss doubled over a temperature increase from 1.5 to 9.5 °C, reaching a mean of 8 % for the highest overwintering temperature. As weight loss could not be accurately measured for most species, we used post-winter weight as an indirect measure of weight loss, controlling for body size and concentrating on dry weight to isolate metabolic effects (decreasing energy storage) from water loss. For effects on post-winter weight there was a significant temperature \times species interaction (Table 1). Negative effects of higher temperatures on weight at emergence were found predominantly for species flying in spring and overwintering as adults (Fig. 2; Table 1), but in different strength. For species flying in summer and overwintering in pre-imaginal stages, winter temperature had positive, negative or no effects on final dry weight (Fig. 2; Table 1).

High overwintering temperature also had an effect on bee phenology (date of emergence), and this response differed significantly among species (Table 1): in some species, adults emerged earlier when they had been exposed to higher temperatures (Fig. 3; Table 1). This also applied predominantly to ‘spring bees’ (advance by ~ 1 – 2 days per °C), while ‘summer bees’ showed delayed emergence or no response (shift by ~ -1 to $< +2$ days per °C). There was also variation in the phenological response to temperature among species within a phenological group. Sexes also responded differently, to a different extent in different

Fig. 1 Loss of fresh cocoon + adult weight (relative to pre-winter weight) in relation to mean overwintering temperature for the two bee species for which it could be measured directly. *Solid lines* show regression predictions from the mixed effects model, controlling for confounding factors (see Table 1). Unlike in Fig. 2, *points* here show the raw data

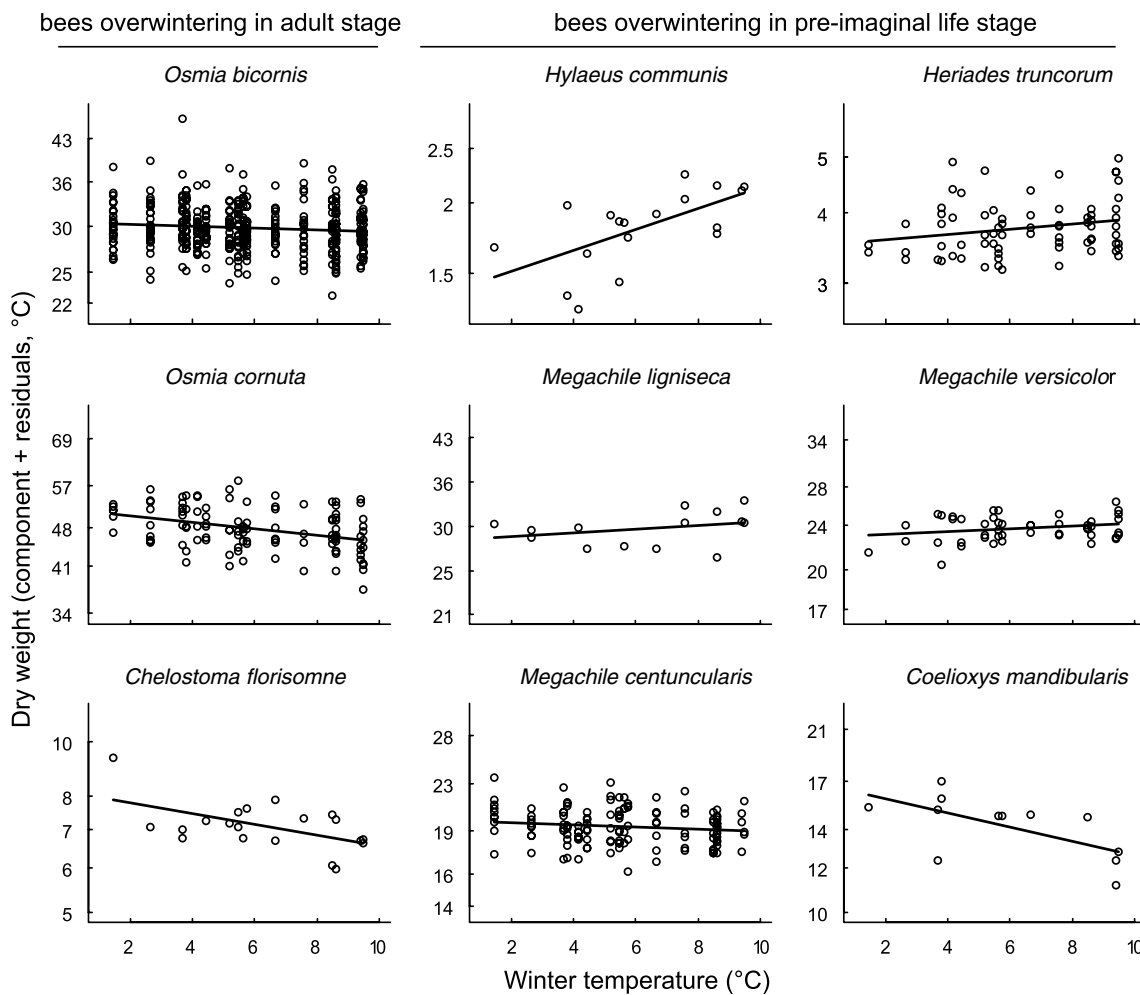
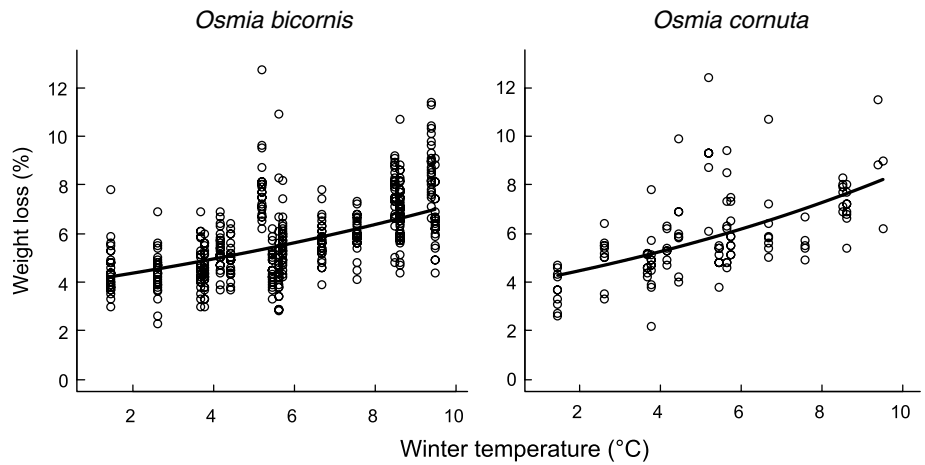


Fig. 2 Dry weight of bees after emergence in relation to overwintering temperature (in climate chambers). Confounding effects of other factors are controlled for in this plot: the y-axis shows partial residuals of a linear mixed-effects model including the additional factors

sex, defaecation and log(head width) (within species). One model was fit for all species, including differences among species and other factors (see Table 1), and this was also used for the *regression lines*. Note the log-scale of the y-axis

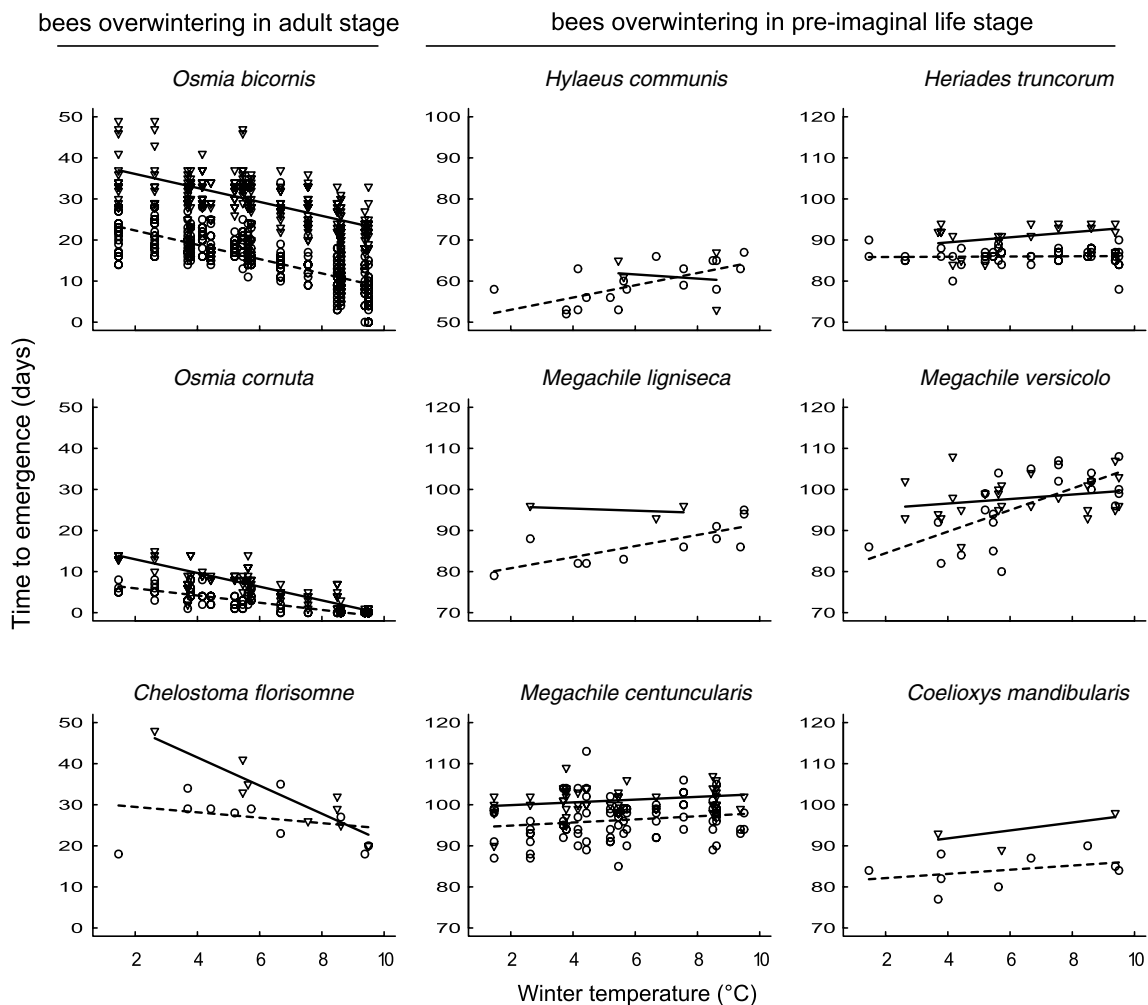


Fig. 3 Effect of overwintering temperature on the time of emergence for nine bee species. Regression lines are shown for sexes separately (males: circles and dashed line, females: triangles and solid line)

from a model fit for all species. y-axis refers to the number of days from the beginning of incubation (1 March 2010). Points show the raw data

species (significant three-way interaction; Table 1). When emergence date responses to temperature differed between sexes within a species, males tended to show less pronounced advance or more pronounced delay than females. The control set of bees that overwintered under outside conditions (temperature: mean 0.76 °C, range –18 to +16 °C, SD = 5.6 °C; humidity: mean 96 %, range 25–100 %) responded similarly to those under experimental conditions (*Osmia bicornis* and *Osmia cornuta*: weight loss slightly higher and emergence earlier than predicted by our models; Online Resource Table S2).

Discussion

In this study, we found that temperature during overwintering affects weight at emergence and the time of emergence

in a number of solitary bee species, and that these species differ in their responses to overwintering temperatures. Interspecific differences in temperature response could be explained partly, but not entirely, by the life-history stage during overwintering.

The increase in weight loss found in a majority of bee species presumably reflects higher metabolic rates and loss of energy. There is a direct effect of temperature on metabolic rates in most organisms (Brown et al. 2004), although the relationship may be weaker in insects during diapause. Effects of overwintering temperature on respiration rate in a solitary bee have been found in a recent study (Sgolastra et al. 2010). This effect may vary with diapause intensity, which, in turn, is influenced by many factors including ontogeny and pre-wintering conditions (Kemp and Bosch 2000; Bosch et al. 2010; Pitts-Singer and Cane 2011; Sgolastra et al. 2011). Differences in diapause intensity

and resulting respiration rate could also explain some of the differences among species including differences in the response to temperature. While *Megachile rotundata*, a bee overwintering as prepupa and active in summer, decreases respiration to a minimum during winter, adult wintering bees probably have a less intensive diapause and already increase respiration by the end of winter (Kemp et al. 2004). This differential temperature sensitivity could explain the generally weaker response in ‘summer bees’ and the strong effect in *Osmia cornuta*, the earliest emerging species in our dataset. For this species, negative effects of higher overwintering temperatures have been found in a previous study (Bosch and Kemp 2004). Even without lethal effects of higher winter temperatures, weight loss during winter probably affects fitness and vigour (Leather et al. 1993). Bosch et al. (2010) have shown that weight loss and fat body depletion entails decreased bee longevity.

It is surprising that the increase of weight loss with increasing temperature not only differently affected different bee species, but post-winter weight even appeared to be positively related to temperature in some species (e.g. *Hylaeus communis* and *Heriades truncorum*). This might be explained by adaptations to warmer winters, temperature-induced changes in diapause intensity or up-regulation of cold-tolerance processes. For example, the production of metabolically costly cryoprotectants such as glycerol is independent of temperature in some insects, while it is a response to low temperatures in others (Leather et al. 1993). Although these issues cannot be resolved without better knowledge of the physiology of the species studied, it became clear that some bee species are more tolerant to increasing temperature than others and thus bee diversity provides response diversity to winter climate warming. Whether this also leads to an insurance effect is uncertain, because that would also require functional redundancy among species (Hooper et al. 2005). As some of the response diversity was correlated to bee phenology, functional redundancy among species with different responses might be limited. However, generalist species with overlapping phenology (e.g. *O. bicornis* and *O. cornuta*), which most likely show some functional redundancy, also differed in their responses.

High overwintering temperature also had an effect on bee phenology—in some species, bees emerged earlier when they had been exposed to higher temperatures, as generally predicted (Gordo and Sanz 2005; Memmott et al. 2007; Hegland et al. 2009), and reported for a few bee species in experimental studies mainly focusing on post-wintering temperatures (Kemp and Bosch 2000; White et al. 2009; Sgolastra et al. 2011). Similar to the results for weight loss, the generally predicted effect of temperature on emergence was predominantly found in ‘spring bees’ (consistent with Bosch et al. 2000; Bosch and Kemp 2003,

2004; Sgolastra et al. 2010), while ‘summer bees’ showed delayed emergence or no response. The importance of overwintering life-history stage for species’ response to climate change has been stressed for other holometabolous insects such as butterflies (WallisdeVries and Van Swaay 2006), but previous studies on bees’ response to climate change have barely considered species overwintering as larvae (Willmer 2012), which we found to respond differently to adult overwinterers. However, species within each group also responded differently to temperature treatments. Again, while the overall stronger effect on ‘spring bees’ can be explained by their less pronounced diapause (Kemp et al. 2004), the tendency to delayed emergence in ‘summer bees’ is difficult to explain. Although advanced mathematical models of emergence-response to temperature have been developed and the accumulation of degree-days is a useful concept to predict the time of emergence (White et al. 2009; Forrest and Thomson 2011), the underlying biological mechanisms are not really known. The degree-day concept implying that the time to completion of development depends on the temperature-dependent metabolic rate is less applicable for low temperatures and when diapause is involved. The delayed emergence after higher winter temperature in some species might be explained by relatively low temperature optima for their prepupal development, leading to slowed development under higher temperatures. Similar effects have been observed for prepupal (summer) diapause in *Osmia* (Kemp and Bosch 2005; Radmacher and Strohm 2011; Sgolastra et al. 2012). This underscores the findings that the timing of climate warming is very relevant for phenological consequences (see also Fitter and Fitter 2002; Visser and Both 2005).

Phenological shifts caused by climate change may have multiple effects on organisms. Interestingly, the degree of protandry (i.e. males emerging before females) was reduced for several bee species in our experiment. Effects of temperature on synchrony of emergence have been reported by previous studies (Krunic and Hinks 1972; Richards et al. 1987). While the observed effect might be influenced by some *Osmia cornuta* males that emerged already during the winter under warmer treatments and were thus missed in our analyses (which considered only bees emerging after the start of incubation), sex-specific phenological responses were also found in other species that did not show emergence during winter. This change in the relative appearance of the different sexes might influence mating behaviour, which is related to territoriality, nesting behaviour and reproductive fitness in bees (Eickwort and Ginsberg 1980).

Our findings also complicate the predictions about climate change consequences for plant–pollinator interaction networks and potential temporal mismatches (Memmott et al. 2007; Hegland et al. 2009; but see Bartomeus et al. 2011). While species responded differently in our study,

species with a similar phenology also showed more similar phenological shifts in response to warming. This might lead to a temporal gap in bee activity. Phenological mismatches might be limited if early blooming plants also show stronger advances in flowering than late blooming species, which has been found in some plant studies (Miller-Rushing and Primack 2008; Rafferty and Ives 2011; Bartomeus et al. 2011).

For accurate predictions, the timing of warming is important, and temperatures will probably change to different extents in different seasons (Christensen et al. 2007). This could also change winter duration, which can have severe consequences for bees (Bosch and Kemp 2004) aside from effects of winter temperature. Variable temperatures or realistic temperature curves might have different effects than constant temperatures (Leather et al. 1993). In this study, we focus on differences in mean temperatures in order to have a feasible number of replicates and to avoid confounding thresholds with variability or specific temperature histories. Weight loss and time of emergence of bees in the outside control did not deviate strongly from predictions based on mean temperature, suggesting that overwintering under experimental constant temperature can be used as a reasonable estimate of responses under natural conditions. A recent study by Bartomeus et al. (2011) used observational data and found larger phenological advances of spring bees per degree of temperature increase than our study. While they considered recent climate change across all seasons and found the strongest effects for April temperatures, we isolated the effect of winter temperature change. Our experimental approach has the further advantage that it is independent of field observations focusing on flowers, which might underestimate the degree of temporal mismatches (see also Forrest and Thomson 2011). Compared to previous experimental studies considering temperature effects on bees, we used a more realistic temperature gradient within the range of climate change predictions.

Our results show that bee diversity represents response diversity with respect to overwintering temperatures, suggesting a potential for an insurance effect (Thomas et al. 2004) of bee biodiversity for pollination (Winfree et al. 2007; Winfree and Kremen 2009). These differences are partly (but not completely) determined by the life stage during winter and likely corresponding differences in diapause intensity, which mediates differential temperature sensitivity. Therefore, future studies focusing on the relationship between temperature sensitivity and functional redundancy of different bee species (including soil-nesting species, for which overwintering has not yet been studied) are needed to fully evaluate the insurance potential of bee diversity for pollination. More generally, this highlights that relationships between response and effect traits deserve to be studied in more detail. It should also be kept in mind that our

experimental results show among-species differences that are potentially functionally relevant, but cannot be used to predict pollination function under climate change in natural communities, because many factors (e.g. plant responses) also influence that. The results on how winter temperature affects the time of emergence are also important for estimating the consequences of phenological shifts caused by warming. Future studies on this topic should consider that bee phenologies respond to (winter) warming, but these responses cannot be assumed to be independent of a species' original phenology. Our study shows that climate warming may also affect bees during the season when they are inactive, and it highlights the need for deeper biological knowledge for predicting consequences of climate change.

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